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ENVIRONMENTAL GRADIENTS AND VEGETATION STRUCTURE ON SOUTH TEXAS COASTAL CLAY DUNES

KERN EWING
College of Forest Resources, Box 354115, University of Washington, Seattle, Washington 98195

ABSTRACT

Clay dunes are unusual geological features that occur near playas, lagoons, or flats that are sometimes wet but dry out annually. If the sediment in these ephemeral bodies of water contains clay, and if there are strong prevailing winds, flakes or granules of clayey material are transported during the dry season and are caught by edge vegetation. The clay particles moisten in the dew or rain and stick together, eventually creating dunes that support vegetation. Known locally as *lomas,* the clay dunes along the Gulf coast of Texas and Mexico reach their greatest stature near the mouth of the Rio Grande River, where this study was carried out. These dunes support ecologically unique vegetation assemblages. They sit, like islands, in hypersaline lagoons. Sharp environmental gradients separate halophytes from typical coastal thornscrub vegetation. Endangered animal species such as ocelots live in the thornscrub. Development pressures along the border threaten their existence, and the construction of artificial *lomas* has been proposed. In this paper I characterize four *loma* plant communities. The first community is found in the adjacent hypersaline *Flats,* and is limited to halophytes. The second community is found in lower but still elevated salinities at the *Edge* of the *lomas.* At low salinities atop the *lomas* are the dense *Thornscrub* community, and a *Mixed Halophyte and Thornscrub* community that is hypothesized to be the result of disturbance. Analysis of elevation and salinity at plots along transects through the *lomas* allows me to correlate individual plant species with salinity preferences and community membership. An interesting outcome is that while a number of species have fidelity to one community type, there are quite a few bridging species that are found in two community types. This information has important implications for the degree of precision required when attempting to restore or create the clay dune ecosystem.

The clay dunes that occur along the Laguna Madre on the southern part of the Texas Gulf coast are interesting both geologically and biologically. Clay dunes are found in association with playas in west Texas and New Mexico, and are reported in Australia and Africa. The coastal clay dunes described in this paper reach their greatest stature and number near the mouth of the Rio Grande River and decrease to the north and south. Similarly, the vegetation of the south Texas delta of the Rio Grande is unique and in some places luxuriant, but diminishes as the distance from both the river and the Gulf increases.

The clay dunes, or *lomas* as they are known locally, are rendered more exotic by the fact that they exist as low hills with non-halophytic vegetation, sitting in the middle of extensive hypersaline wind tidal flats or lagoons. The lagoons are periodically inundated by wind tides or hurricanes, but are subjected to long periods of drying in the hot south Texas climate. Salts concentrate and the surface of the lagoons may become dry. In addition to the salinity and periodic droughts, there is a persistent brisk wind out of the southeast for much of the year. In this semiarid, semitropical climate, the warm months may be generally described as any but January and February, and even during these months, daytime temperatures above 30°C are common.

Lomas near Boca Chica, the beach north of and adjacent to the mouth of the Rio Grande River, are covered with thornscrub vegetation, some of which is commonly found over much of the Tamaulipan biotic province. In addition, species characteristic of the *lomas* and other coastal areas are found, including *Citharexylum berlandieri* Robins., *Maytenus texana* Lundell, *Prosopis reptans* Benth., *Echeandia chandleri* (Greenm. & Thomps.) M. C. Johnst., *Monanthochloe littoralis* Engelm., and *Yucca treculeana* Carr. Most of the *lomas* in the Boca Chica area are named, and the site for this work is called *Loma Tio Alejos.* It has a roughly north-south orientation, is 200 to 300 meters wide by 600 meters long, and rises about 7.5 m out of a lagoon, which is at an elevation of about 1.5 m. The south end of the *loma* is 300 meters north of a bend in the Rio Grande River; the east side is about 12 km from the Gulf of Mexico. This site and much of the surrounding land is now part of the Lower Rio Grande Valley National Wildlife Refuge.

It has long been known that non-halophytic vegetation grows on *lomas,* and that hypersaline marshes and flats surround them. They are recognized as a unique biotic community by the U.S.F.W.S., and are included in a proposed wildlife corridor running down the Rio Grande and up the coast. One impetus for this study is the extensive restoration program in place on the L.R.G.V. National Wildlife Refuge and the potential for constructing or restoring *lomas* to create habitat. Off-refuge, there are significant pressures from encroaching commercial and residential development and from the proposed construction of a new international bridge and its infrastructure 8-km west of this site.

Knowledge of typical vegetation composition on *lomas* and the relationships among vegetation, *loma* elevation and soil salinity are critical to understanding what controls the vegetation structure. *Loma* vegetation is known to be dense, and often much shorter than it would be in other locations. In this study I measured vegetation composition, woody plant height and density, canopy cover, elevation and soil salinity in quadrats along transects across *Loma Tio Alejos*. Ordination and classification analyses were performed on cover data. The nature of the relationship between *loma* elevation and salinity was determined, and species affinity to sites was related to salinity and elevation.

Clay dunes. The clay dunes along the Gulf Coast in southern Texas have been remarked upon almost since the first accounts of the exploration of the area, probably because these explorations sought river mouths and disembarked from coastal areas. Coffey (1909), while on a soil survey of the region for U.S.D.A., saw the dunes and hypothesized that they were formed by granules of clay, which were blown off the surface of dried lagoons during hot, windy summers. The particles blew to the edge of the lagoon, were caught by vegetation or by wrack or debris, and began to accumulate. Rainfall or the humidity of the nights caused the particles to coalesce. Coffey further noted that they were found near the Rio Grande because the rains are seasonal and lagoons dry out; in more humid climates such conditions do not occur. Foscue (1932) noted that the dunes looked like small islands covered with brush. Huffman and Price (1949) and Price and Kornicker (1961) compared clay dunes all along the Texas and Mexican coast and determined that they existed along the mainland coast from Soto la Marina River in Tamaulipas, Mexico to St. Charles Bay (at the Aransas National Wildlife Refuge) in Texas. The dunes are highest at the Rio Grande (10 m), and become lower (1 m) in the more humid climates to the north and south. These authors essentially agreed with Coffey about the formation of the dunes, adding that they probably grow only during hot months (March to November), retain a loosely porous structure, and represent about 5000 years of growth since beginning of the current still-stand of sea level. During a seven year period of drought in the fifties, about a foot of loosely consolidated pellets accumulated. Their height made the dunes attractive camp sites for the coastal Indian tribes that fished in the area. Aboriginal artifacts occur from about mid-dune to near the top foot, and European artifacts occur near the top. In addition to their use by humans, the endangered ocelot (Tewes 1982) also uses clay dunes.

Tamaulipan Thornscrub. Brown (1994) describes the Tamaulipan biotic province as being one of several provinces that are semidesert scrublands. Such systems are dominated by thorny shrubs and small trees, and characterize much of the world's tropic-subtropic zones. They are found in Australia (*mulga*), southern Africa (bush), South America (*chaco-seco*), Mexico (*matorral*) and Texas (*chaparral*). They are drought-deciduous communities that occupy a position on a moisture gradient somewhere between desert scrub and woodland or forest. They often have an irregularly layered overstory between 2 and 8 m in height, and are typically composed of spinose, microphyllous, and succulent life forms. Thornscrub is often in competition with grassland, and may increase under grazing pressures, with fire suppression, or on poorer soils.

Muller (1947) observed that east central Coahuila, southern Texas, northern Nuevo Leon and northern Tamaulipas all have a vegetation form that is similar. Shreve (1917) called it Texas semi-desert. Muller proposed that it be called Tamaulipan thorn shrub. The more luxuriant and tree-dominated forms found in south Texas and Tamaulipas were called Tamaulipan thorn forest. These environments differ from the adjacent Chihuahuan desert shrub in that they are found at lower elevations, have more rainfall, and are exposed to winds from the Gulf of Mexico. With these habitat differences are also found more thorny shrubs, an abundance of grasses, more luxuriant growth of shrubs, a richer flora, and more numerous characteristic species. With the increase in species there is also a greater number of variants of the vegetation formation.

Blair (1950) included the area in Texas south of the Balcones fault line (which runs from Austin through San Antonio) in his Tamaulipan province. He described the biota of the province as neotropic, strongly diluted by Sonoran biota characteristic of the southwestern U.S. and parts of Mexico, and by biota characteristic of the forests blanketing the Gulf coastal plain. The climate is semiarid and megathermal. From the coast westward, the brush thins as available moisture declines. In Cameron County, at the southern tip of the state, average annual precipitation is just above 25 inches. Mean maximum temperature is 95° in July, mean minimum is 51° in January. Rainfall peaks during tropical storm season (centered on September). Long periods of drought, during which there is little or no rain for 4–6 months, are common; periods during which drought years occur for 3–5 years in succession are also common. A strong, persistent hot wind blows out of the southeast for much of the year.

Probably the earliest exhaustive description of the thornscrub vegetation of the Rio Grande delta was given by Clover (1937). Later Blair (1950), in his delineation of the biotic provinces of Texas, would call the area on the floodplain the Matamoran district of the Tamaulipan Biotic Province. Clover justified the use of the term *chaparral* for the shorter vegetation of the area, saying that it referred to *chaparro prieto* (*Acacia rigidula* Benth.). *Mesquital* is the term used for *Prosopis glandulosa* Torrey-dominated communities, and *sacatal* for grasslands. Currently, two general types of brush habitats are recognized in the area. The first is referred to as riparian and scrub forests (associated with the Rio Grande, and producing taller vegetation); the second is upland thornscrub and thorn woodland (Jahrsdoerfer and Leslie 1988).

Clover (1937) described the vegetation of the clay dunes near the coast as being similar to salt-affected thornscrub nearby, but being composed of shrubs twisted by the heavy winds. Dominants listed were *Pithecellobium ebano* (Berl.) C. H. Mull., *Leucophyllum frutescens* (Berl.) I. M. Johnst., *Ziziphus obtusifolia* (Torrey & A. Gray) A. Gray, *Castela texana* (T. & G.) Rose, *Randia rhagocarpa* Standl., *Forestiera angustifolia* Torr., *Prosopis glandulosa* Torr. and *Celtis pallida* Torr. Between the clay dune "islands" and the main *chaparral-mesquital* was a transition zone and *sacahuistal* (dominated by *Spartina spartinae* (Trin.) Merr.). USFWS (1997) added *Citharexylem berlandieri, Erythrina herbacea, Dalea scandens* (Mill.) R. T. Clausen, *Echeandia chandleri* and *Sporobolus tharpii* Hithc. as being found exclusively in or near the *loma*-coastal brushland community. Johnson (1963) added that the windward sides of some of the dunes were covered with a thick growth of *Sporobolus wrightii* Scribn. (*sacatón*).

Methods

In late October 1998, I began the establishment of two transects across *Loma Tio Alejos.* The first transect ran approximately east-west. It started in an unvegetated area of hypersaline lagoon to the west of the *loma,* crossed 200-m of halophytic vegetation, encountered the southern part of the *loma* and entered thornscrub vegetation. It climbed for the next 100 m to the ridgeline and then dropped, over the following 100-m, to the edge of halophytic vegetation on the east of the *loma.* The transect then ended after it traversed 30 m of the halophytic vegetation. Rather than being symmetrical, the *loma* is kidney-bean shaped, so that transect two could be oriented in a north-south direction and cross the north end of the *loma* almost perpendicular to its axis.

The second transect was finished by the beginning of December. It started on the south side of the north end of the *loma* and traveled for 30 m in halophytic vegetation, then entered the brush and traveled 80 m to the ridgeline. It then went down through a depression and up to another ridgeline, traversing extremely dense brush for about 70 m. The transect descended through thornscrub for 70 meters and was terminated about 50 m into the halophytic vegetation to the north of the *loma.*

Distance along transects was measured with surveying tapes, and station stakes were placed every ten meters (stations 0+00, 0+10, etc.). Differential leveling, employing a Keuffel and Esser optical level, was used to determine relative elevations along each transect. Elevations on transect one were tied to elevations on transect two by closing a leveling loop from one transect to the other along a trail which ran down the ridge of the *loma.* The elevation of the transects was then fitted to a USGS contour map of the *loma* and elevations from that map were used to register the high and low points surveyed.

Vegetation was sampled in 10 × 20 m quadrats along most of both transects vegetation was so thick from station 0+20 to station 2+00 along transect 2 that it was sampled using 5 × 20 m quadrats oriented with their long axis parallel to the machete-cut line through the brush. By the conclusion of the investigation, 57 quadrats were measured and 76 plant species were found. In each quadrat the percent cover of herbaceous species was recorded, as well as the number of species, the number of individuals of each woody species, height and two crown-width dimensions for woody species. Cover for woody species was calculated by averaging the two dimensions and calculating the area of a circle with this average as the diameter.

Soil samples for salinity measurements (Abbott 1967) were taken from each quadrat using a 3.8-cm diameter corer. Cores were generally 10–15 cm long, and were taken after removing organic matter and debris from the soil surface. Cores were extruded onto a tray and the length of each sample was measured, allowing the calculation of soil volume. Wet weight of each core was measured, all were oven-dried at 80°C, and dry weights were measured. Dried cores were placed in flasks and a volume of water twice the original volume of the cores was added to each. The flasks were sealed with rubber stoppers and agitated for three days. They were then allowed to settle in a cold room for three days and the clear supernatant was removed with a syringe.

Osmolality of the soil extract was measured with an Advanced Instruments Model 3300 Micro Osmometer (Advanced Instruments, Inc, Two Technology Way, Norwood, MA 02062). From the osmolality of the soil extract, values were calculated for the osmotically active solutes per unit volume of soil ("a" below) and the apparent salinity of the soil solution at the time the sample was taken ("e" below) (Mahall and Park 1976). The following calculations were made to arrive at these two values.

$$a = \frac{b \times c}{d} \qquad e = \frac{b \times c}{f}$$

where a = osmotically active solutes per unit volume of soil (m-osm. ml^{-1});
b = osmolality (m-osm. ml^{-1} water) of soil extract (from freezing point depression);
c = volume of water added to dry soil core (ml);
d = original volume of soil core (ml);
e = apparent salinity of soil solution (m-osm. g^{-1} water);
f = weight of water in soil core (g).

The soil solution salinity was converted to ppt for figures.

Two data sets, one containing species cover information for each quadrat and the second containing elevation and soil salinity data at each quadrat were entered as the primary and secondary matrices in the multivariate software package PC-Ord (McCune and Mefford 1997). Classification was performed using TWINSPAN, and ordination was performed using DCA (detrended correspondence analysis), which uses the stand species matrix; the joint plot option was used to overlay environmental variable vectors over the DCA-generated ordination plot.

TWINSPAN is a divisive classification technique that divides all initial stands in an analysis into two groups using an ordination, then iteratively refines the division. Each group formed is then divided into two new groups. (Jongman et al 1987). The mechanical division of existing groups can go on until some stopping rule is triggered (maximum number of divisions or minimum number of stands in a group may be specified). The actual selection of what divisions to accept may depend upon whether further divisions add to the explanatory power of the analysis (Gauch 1982). In this analysis, four groups were used because each of the four groups represented a homogeneity of species composition and was characterized by similar dominant species.

Results

Elevation. The elevation of the saline flats around the *lomas* in this area is about 1.5 m, USGS datum. On this *loma,* over a distance of 100–150 m, the measured transects rose to about 6.5–7 m at the height of land, then dropped again (Fig. 1). The elevation of the highest point on the *loma* was estimated at about 9 m.

Vegetation. Seventy-six species were found within the sampling quadrats along the two transects across *Loma Tio Alejos.* Twenty-seven of them were erect, woody plants. There were also 8 grasses, and a number of halophytes, weedy herbaceous species, and herbaceous understory species. *Echeandia chandleri,* a lily limited to clay soils in south Texas and described as rare (USFWS 1997), was common here. *Ophioglossum vulgatum* L., a vascular cryptogam, was found growing under *Prosopis glandulosa* trees. The vegetation gradient from the saline flats to the thornscrub of the *lomas* was short and steep, but there was surprising overlap of thornscrub and halophytic species.

Vegetation composition and cover data were analyzed using multivariate analysis. Classification of stands and species was accomplished using TWINSPAN. One of the products of a TWINSPAN analysis is a joint ordination of stands and species called a two-way table. The species list from a two-way table is ordered, i.e., the species that are on either end of the list are usually found in completely different environments and species which are next to one another on the list are usually found together. On the list in Table 1, species at the top are from sites near the highest elevations of the *loma,* while species at the bottom occur mostly in the adjacent flats and at the *loma* edges.

I elected to stop the TWINSPAN procedure after four groups of stands had been generated because each of the four groups represented a relatively homogeneous association of species and was characterized by a unique dominant species or group of dominants. I will describe the important species, the location of stands, and the general environment in which each group occurs.

The first division segregated the high-diversity, non-halophytic thornscrub vegetation into one group. Woody thornscrub species and their associated herbaceous understory or gap species dominate it. The other group from this division includes all of the species known to be halophytic, but halophytes are not limited to the second group.

The second division divided stands in the thornscrub vegetation group into two smaller groups, one of which is made up of species characteristic of more widely distributed coastal upland sites. All of the sites in this subgroup are found on the higher elevations of the north transect; the vegetation there is characterized by a dense canopy and shortened stature. On Figure 2, this association is called "*Thornscrub*". The other subgroup in this division includes more salt-tolerant thornscrub which is found on the lower ends of the north transect and on the south transect. On Figure 2 this association is called "*Mixed Thornscrub and Halophytes*". Indicator species for the group are *Prosopis reptans, Maytenus texana* Lundell. and *Ericamera austrotexana* M. C. Johnst. Almost all of the *Yucca treculeana* Carr. and *Prosopis glandulosa* are also found in this grouping. This second subgroup could be further divided into closed canopy and open canopy groupings, which would have slight species differences.

The third division divides the stands containing mostly halophytic vegetation into two subgroups. The first subgroup is the association that makes up the low shrubby vegetation around the edges of the *loma.* On Figure 2 this is called "*Edge*". Indicator species for this subgroup are *Borrichia frutescens* (L.) DC and *Lycium carolinianum* Walt. The sec-

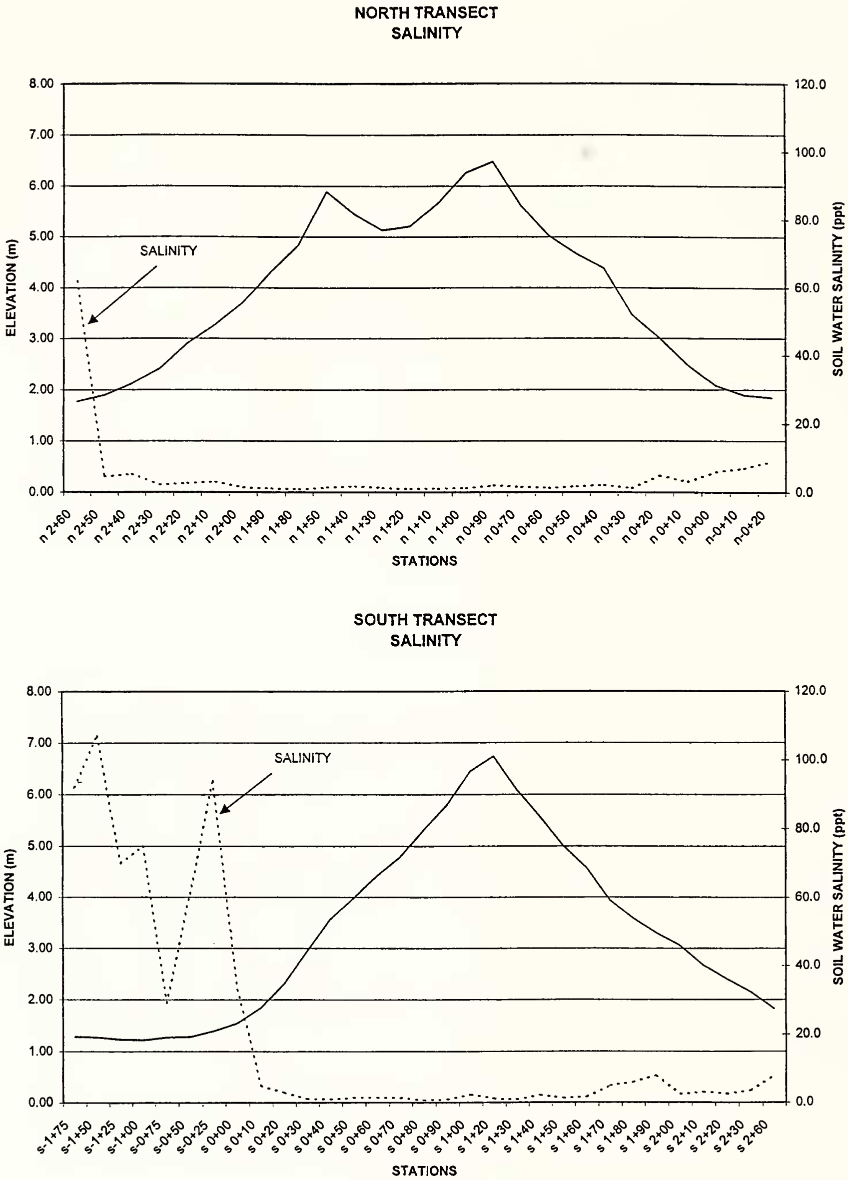

FIG. 1. Elevation and salinity along the north transect (which runs north-south) and the south transect (which runs east-west) across *Loma Tio Alejos,* near the mouth of the Rio Grande River in south Texas. Salinity is represented by a dashed line, elevation by a solid line. The salinity is the apparent soil water salinity obtained by measuring the osmolality of a known volume of water into which a dried soil sample was mixed; salinity at the water content of the soil when the sample was taken was then calculated.

ond subgroup is dominated by three species (*Salicornia virginica* L., *Monanthochloe littoralis* Engelm. and *Batis maritima* L.) and little else; sites making up this subgroup occur in the extremely salty flats surrounding the *lomas.* On Figure 2 this association is referred to as "*Flats*".

The same data set that was used to obtain a classification of stands and species with TWINSPAN was subjected to an ordination analysis. Ordination allows the investigator to plot stands or species in a multi-dimensional space that can be interpreted in terms of environmental variation; Detrended Correspondence Analysis (DCA), an indirect ordination technique, was used. Since an environmental matrix of stands by environmental data (salinity, elevation) was available, the joint plot option of PC-Ord was used to plot environmental vectors on the DCA ordination plots. The first DCA axis had and an eigenvalue of 0.859, indicating that a substantial amount of the variation in the data set was accounted for by this axis. When plotted as a joint plot, the arrow representing salinity was almost identical to axis one, and the arrow representing elevation, while negatively correlated with salinity, was very close to axis one.

Canonical Correspondence Analysis (CCA) allows the investigator to constrain the ordination axes to some combination of directly measured environmental variables (Jongman et al. 1987). When this was done using elevation and salinity as the environmental variables, the eigenvalue for the first axis was 0.662, which is still high (Jongman et al. 1987). In the CCA analysis the arrows for elevation and salinity were highly correlated with axis 1. The results of these ordinations indicate that elevation and salinity are environmental factors that account for most of the variation in vegetation structure on the *lomas.* They are inversely correlated; as elevation increases, salinity decreases.

Salinity. Salinity was high in the flats but dropped very quickly as the *loma* elevation rose above that of the surrounding flats. (Fig. 1). Salinity per volume of soil and apparent salinity of soil water were highly correlated ($r = 0.995$), so apparent salinity in ppt will be used to discuss the relationship among elevation, vegetation and salinity. Average soil water salinity in plots in the "*Flats*" vegetation association was 64.1 ± 11.8 ppt. This salinity is significantly ($P = 0.05$) greater than that in any of the other associations. Mean soil water salinity in the "*Edge*" association, 6.3 ± 1.9 ppt, is higher than that in the "*Mixed*" or "*Thornscrub*" groups, though not significantly so. Mean salinity in the "*Mixed*" group is 2.1 ± 0.4, and in the "*Thornscrub*" group is 2.0 ± 0.3 ppt.

Discussion

The ecotone between the hypersaline flats of Laguna Madre and the coastal thornscrub in south Texas has created interesting and unexpected vegetation associations. The *lomas* or clay dunes are a microcosm of this contact, and they reach their maximum expression near the mouth of the Rio Grande River. Coastal thornscrub on the *lomas* and on the nearby mainland is valued because of its importance as wildlife habitat (ocelots, birds, and butterflies). It is part of a breathtaking diversity of vegetation; Jahrsdoerfer and Leslie (1988) indicated that there were 265 native woody species in the thornscrub of southern Texas. It is the site of scarce and unusual plant species including the species of concern *Echeandia chandleri, Citharexylum berlandieri* Robins. and the endemic *Sporobolus tharpii* Hitchc. (Jahrsdoerfer and Leslie 1988). The Laguna Madre is unique in that it is a huge lagoon, which has little freshwater input except from tropical storms. The hot climate, persistent winds and a tendency to experience prolonged periods of drought have created a water body that becomes hypersaline. Many of the *lomas* near the site of this study rise out of wind flats at the edge of the Laguna Madre; these flats are sometimes inundated but are very salty during most years.

Many of the *lomas* near the mouth of the Rio Grande and behind Boca Chica beach are now protected and part of the Lower Rio Grande Valley National Wildlife Refuge. This refuge and the Laguna Atascosa National Wildlife Refuge on the coast 20 km to the north are both sites of active vegetation restoration programs. Because of the sharp environmental gradients in areas adjacent to salt flats and lagoons, and because of unique tolerances and preferences of plant species which would normally be selected for restoration plantings (in general, dominant and secondary woody species), information about the sorting of species along environmental gradients is important. Since the *lomas* rise like small islands out of low and level salt flats, their elevation was predicted to be an important environmental axis; this proved to be the case. Since *lomas* support species common to sites that are not salt-affected, and because they are surrounded by halophytic vegetation that is tolerant to high concentrations of salts, a salinity gradient was predicted. This also proved to be true.

Other environmental factors may also shape vegetation structure. Winds off the nearby gulf are persistent and may result in dwarfing of vegetation. Soils sampled were generally silty clays or clayey silts, with more clay in soils in the flats. *Lomas* have a history of use by people, and there are roads leading to them, around them and across them. There are excavation sites, dumps, and disturbed areas with weedy vegetation (primary weeds are the introduced pasture and lawn grasses *Cenchrus ciliaris* L., *Cynodon dactylon* (L.) Pers., *Dichanthium annulatum* Stapf. and *Panicum maximum* Jacq.); some of the vegetation plots occurred in these areas. Multivariate analysis indicated that elevation and salinity change explains a very high amount of the variation in vegetation on *Loma Tio Alejos.*

The analysis of data from 57 quadrats along two transects across the *loma* was carried out by performing a classification procedure (TWINSPAN) and an ordination procedure (DCA). As a result of the TWINSPAN analysis, four vegetation groupings or associations were identified. The groups were called "*Thornscrub*", "*Mixed Thornscrub and Halophytes*", "*Edge*" and "*Flats*". The 16 plots in the *Thornscrub* group contained 36 plant species. For *Mixed Thornscrub and Halophytes* the numbers were 20 plots and 67 species, for *Edge* 13 plots and 41 species, and for *Flats* 8 plots and 11 species.

All except one of the plots assigned to the *Thornscrub* group were on the north transect; that one occurred in very thick brush on the south transect. This association is made up of plants in very dense, short (3–4 m) vegetation. Vegetation on the north transect may have been subjected to greater wind intensity, because the south part of the *loma* is partially protected from the wind by vegetation along

TABLE 1. LIST OF SPECIES FOUND ALONG TRANSECTS AT *LOMA TIO ALEJOS*. Species have been ranked by TWINSPAN classification program so that those generally found at the higher elevation, lower salinity sites occur at the top of the list; those found at the lower elevations and in the saline flats are at the bottom. Frequency of occurrence in plots of each of the four TWINSPAN community types at the site (*Thornscrub, Mixed Thornscrub and Halophytes, Edge and Flats*) is shown for each species as a percentage. Numbers of plots of each of the community types are respectively n = 16, 20, 13 and 8.

	Thornscrub	*Mixed*	*Edge*	*Flats*
Castela texana	44	10	0	0
Pithecellobium pallens	6	0	0	0
Malpighia glabra	25	5	0	0
Bastardia viscosa	31	5	0	0
Rivina humilis	50	20	0	0
Celtis pallida	63	30	8	0
Pithecellobium ebano	19	0	0	0
Phaulothamnus spinescens	81	45	8	0
Randia rhagocarpa	69	10	0	0
Lycium berlandieri	13	5	0	0
Aloysia gratissima	13	0	0	0
Citharexylum berlandieri	94	85	8	0
Zanthoxylum fagara	100	85	0	0
Karwinskia humboldtiana	63	35	8	0
Lantana horrida	38	60	0	0
Capsicum annum	6	20	0	0
Schaefferia cuneifolia	25	40	0	0
Passiflora foetida	6	5	0	0
Cissus incisa	44	60	8	0
Forestiera angustifolia	19	30	8	0
Verbesina microptera	38	30	0	0
Zisiphus obtusifolia	13	20	8	0
Isocoma drummondii	19	80	15	0
Allowissadula lozani	19	55	8	0
Yucca treculeana	13	60	15	0
Prosopis glandulosa	25	85	8	0
Eupatorium azureum	50	70	8	0
Leucophyllum frutescens	38	65	8	0
Condalia hookeri	6	10	0	0
Echeandia chandleri	13	25	0	0
Gymnosperma glutinosum	6	10	0	0
Ericameria austrotexana	0	80	8	0
Eupatorium incarnatum	0	20	0	0
Cenchrus incertus	0	10	0	0
Atriplex acanthocarpa	0	5	0	0
Wedelia hispida	0	15	0	0
Physalis cinerascens	0	20	0	0
Ophioglossum vulgatum	0	20	0	0
Acacia farnesiana	0	5	0	0
Trixis inula	0	5	0	0
Dichanthium annulatum	0	40	0	0
Croton cortesianus	0	5	0	0
Sida ciliaris	0	10	0	0
Malvastrum americanum	0	15	0	0
Ibervillea lindheimeri	0	10	0	0
Chenopodium ambrosoides	0	5	0	0
Cenchrus ciliaris	0	50	15	0
Sarcostema cynanchoides	0	30	15	0
Cynodon dactylon	0	10	8	0
Croton leucophyllus	0	10	8	0
Opuntia leptocaulis	6	30	31	0
Trandescantia micrantha	6	10	23	0
Acleisanthes obtusa	6	5	8	0
Borrichia frutescens	13	55	85	0
Oxalis drummondii	0	5	8	0
Solanum eleagnifolium	0	10	8	0
Sporobolus wrightii	0	10	15	0
Panicum maximum	0	5	0	13
Oxalis dichondrifolia	6	15	15	0

TABLE 1. CONTINUED.

	Thornscrub	*Mixed*	*Edge*	*Flats*
Evolvulus alsinoides	0	5	8	0
Maytenus texana	0	75	77	13
Prosopis reptans	0	70	85	25
Machaeranthera phyllocephala	0	45	46	0
Spartina spartinae	0	10	15	0
Suaeda linearis	0	0	23	25
Cressa nudicaulis	0	10	23	25
Salicornia virginica	0	0	23	100
Talinum paniculatum	0	5	8	25
Atriplex matamorensis	0	0	0	13
Lycium carolinianum	0	20	85	0
Limonium nashii	0	0	31	0
Echinocactus setispinus var. setaceus	0	0	8	0
Distichlis spicata	0	0	8	0
Monanthochloe littoralis	0	30	100	75
Opuntia engelmannii	0	10	38	13
Batis maritima	0	5	69	100

the river and by a road berm. Plots assigned to the *Mixed* group occurred in a more disturbed area on the north end of the north transect, and at the upper elevations of the south transect. There was erosion and open areas in both locations, so human disturbance may have been partially involved in the creation of such sites. Since salinity and elevation differences were inconsequential between plots in these two associations, the hypothesis that the *Mixed* association is generated by disturbance should be investigated more thoroughly. Any restoration attempt would create a disturbed environment, and so the *Mixed* association might be the expected mid-successional vegetation type on less-salty soils. *Prosopis glandulosa,* well-known as a self-seeder on open sites in South Texas (Archer et al. 1988), is a dominant species in the *Mixed* association but found in few plots in the more dense *Thornscrub* association.

Plots in the *Edge* association occur in a band about 30–40 m wide around the *loma,* and are visually different from the adjacent brush because they are open, and woody vegetation in them is either short or widely spaced. At the lower and saltier sites in this association, plant diversity diminishes to an average of 4 species per plot, and plants are generally less than a few decimeters tall. The saline *Flats* are characterized by a few species, and in places the salinity may become so great that no vascular plants occur. There was a substantial increase in soil salinity at the interface between the *Edge* association and the *Flats* (Fig. 1). At one unvegetated quadrat in the flats, a soil water salinity of 187 ppt, roughly five times that of sea water, was measured.

The mean soil water salinity of soil samples taken from plots in the *Flats* was 64 ppt, or almost twice the salinity of seawater. The *Flats* are truly the province of halophytes. Localized or general evaporation and concentration probably result in much higher localized salinity during drought periods. Salinity in the *Mixed* and *Thornscrub* associations, on the other hand, fell under or around the 1.5–2 ppt salinity threshold that is generally considered the point below which crop plants have no salinity problems (Hartman et al. 1990). Salinity in plots in the *Edge* association were generally in the range within which plants are likely to be affected, but not so high as to limit plant composition to halophytes.

Each of the four vegetation associations identified by classification analysis was characterized by a set of dominant species (based upon total cover). In analyzing the species composition of each association, it became evident that there were some species which preferred conditions found in sites limited to one vegetation association, but there were also many species that did quite well in two of the associations. For instance, *Castela texana* (T. & G.) Rose. and *Randia rhagocarpa* (Fig. 2a) were common in *Thornscrub* association and rare in the *Mixed* association. *Citharexylum berlandieri* (Fig. 2b) and *Zanthoxylum fagara* (L.) Sarg. were in both *Thornscrub* and *Mixed* associations. *Yucca treculeana* Carr. (Fig. 2c) preferred the *Mixed* association, while *Borrichia frutescens* (L.) DC (Fig. 2d), *Maytenus texana* Lundell. and *Prosopis reptans* were found in both *Mixed* and *Edge* associations. This combination of species with fidelity to an association and species which overlap associations continued with *Lycium carolinianum* Walt. (Fig. 2e) found in *Edge, Monanthochloe littoralis* and *Batis maritima* L. (Fig. 2f) found in *Edge* and *Flats,* and *Salicornia virginiana* L. (Fig. 2g) found in *Flats.*

All of the species listed by Shindle and Tewes (1998) as recommended for the restoration of ocelot habitat, as well as a broad variety of others, are found on the *lomas.* This paper has presented information about the environmental preferences of *loma* species. The mixing of species which have

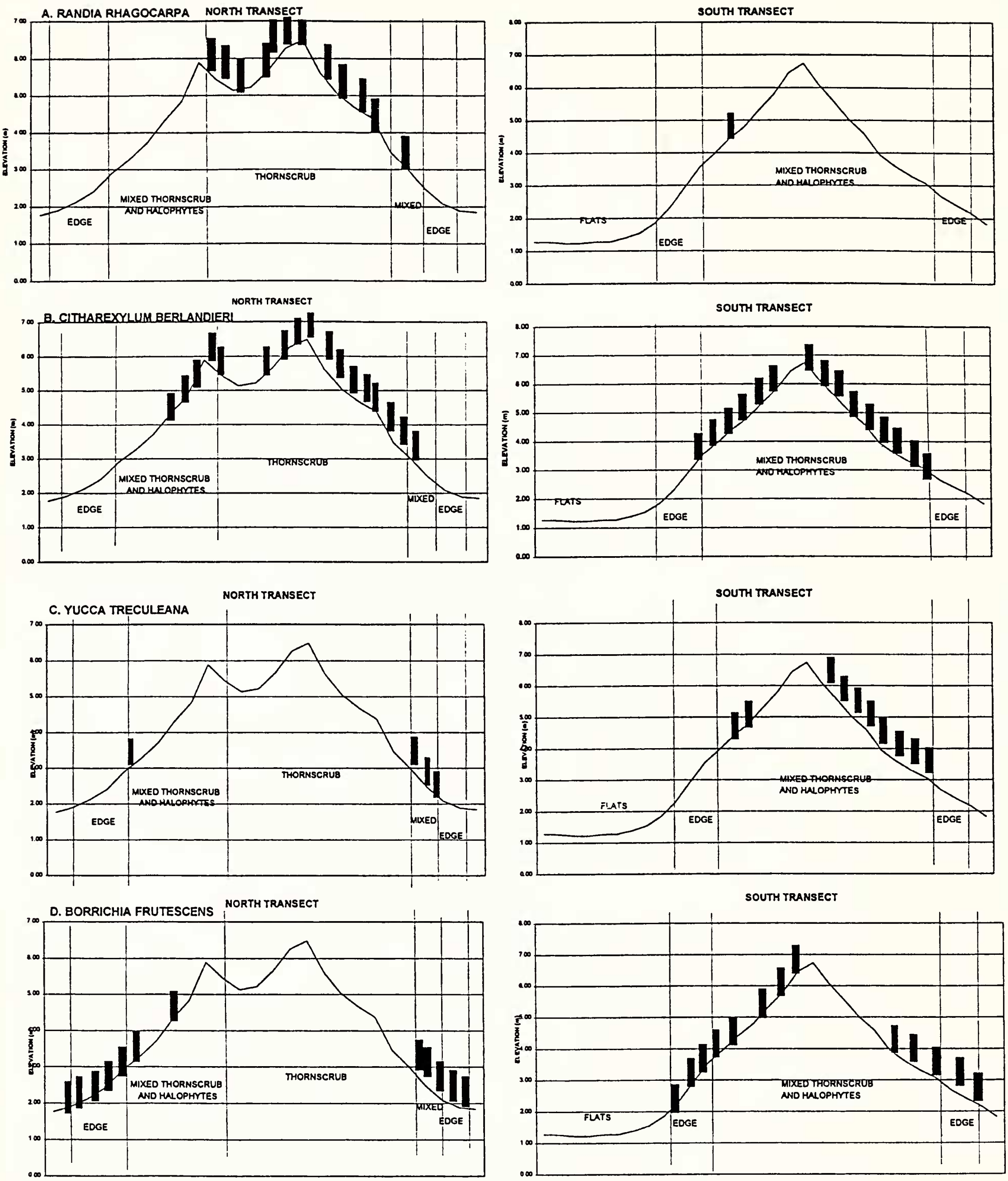

FIG. 2. Presence of species in plots along transects. A solid vertical bar indicates that the species shown was present in a plot: a.) *Randia rhagocarpa,* occurring primarily in the *Thornscrub* association, b.) *Citharexylum berlandieri,* occurring in both the *Thornscrub* and *Mixed* associations, c.) *Yucca treculeana,* occurring primarily in the *Mixed* association, d.) *Borrichia frutescens,* occurring in both the *Mixed* and *Edge* associations, e.) *Lycium carolinianum,* occurring primarily in the *Edge* association, f.) *Batis maritima,* occurring in both the *Edge* and *Flats* associations, g.) *Salicornia virginica,* occurring primarily in the *Flats* association.

narrow habitat ranges with species which have broader habitat ranges when planting a restoration project is wasteful of plant materials. For the plant installation phase of a restoration project, some species may be placed on the landscape with less precision, but others require an exact understanding of the species preferences and the site conditions. Plant materials for restoration or creation of *lomas*

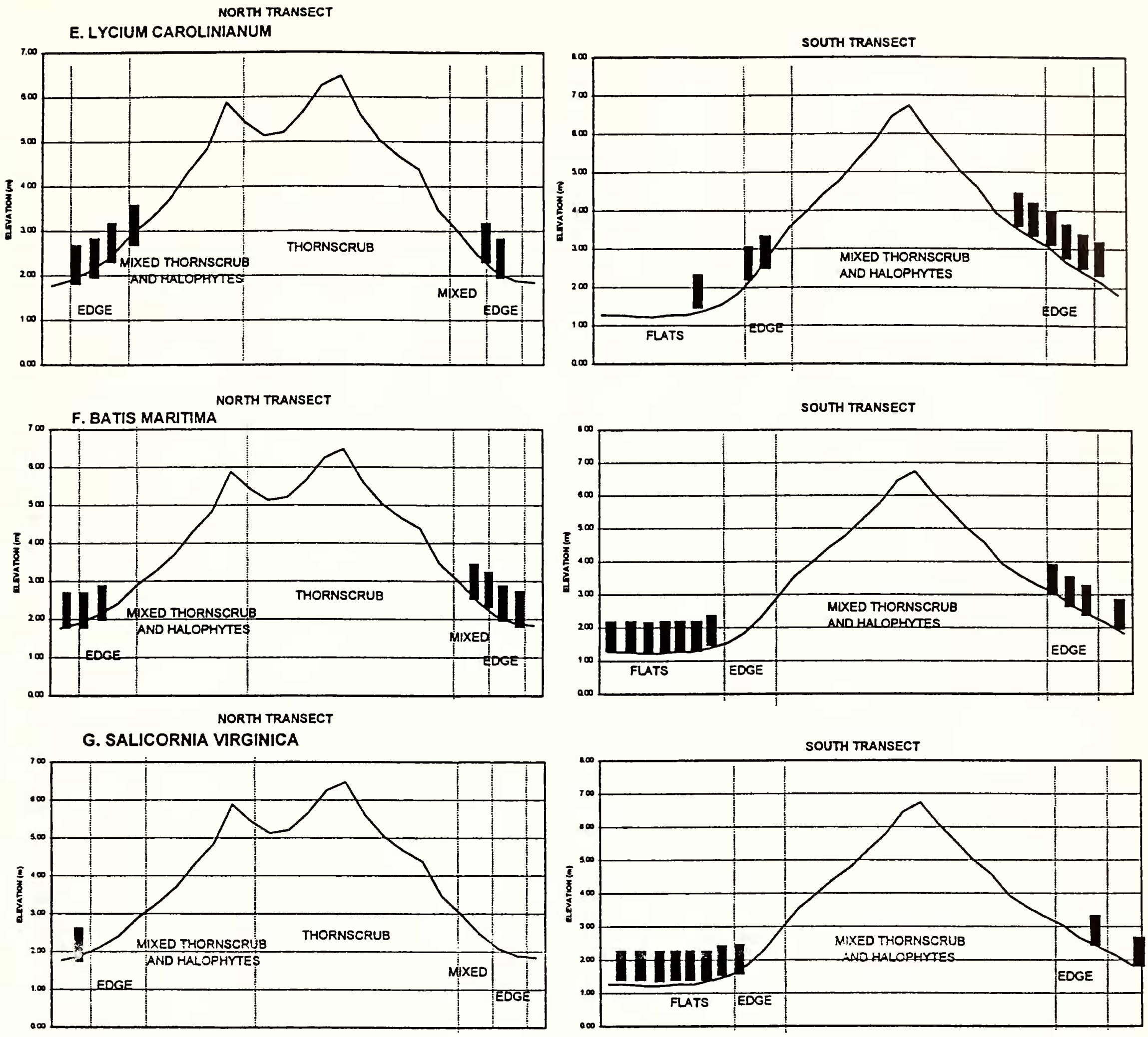

FIG. 2. Continued.

will probably never be abundant, so placement of seedlings or seeds into the proper environmental zone will be critical to the success of a restoration project.

In conclusion, this work has confirmed that coastal clay dunes or *lomas* are unique systems that are persistent over time. Unusual plant associations (thornscrub vegetation and halophytes in close proximity or mixed) and rare and threatened plants (*Echeandia chandleri, Citharexylum berlandieri*) are found on them; their individual vegetation structure can be complex. They are known to be valuable as wildlife habitat. Vegetation structure across *lomas* varies along environmental gradients, which can be predicted for the most part by measuring elevation and salinity. Reports in the literature suggest that wind direction can also be an important factor in vegetation composition and size (Clover 1937). For many centuries, these unique systems have been isolated and not greatly damaged. Population pressure and commercial development now pose a threat to the vegetation systems and the wildlife that they support. Restoration in other areas of south Texas Tamaulipan thornscrub has been undertaken successfully, and the core of an extensive wildlife corridor is being created along the coast and up the Rio Grande River. The restoration or creation of *loma* vegetation to augment habitat and add to the wildlife corridor is an important and achievable element of this restoration.

The ability to restore unique ecosystems like the clay dunes, if indeed we have that ability, does not mean that there is no need for conservation of such unusual habitats. Conservation is an integral part of the U.S.F.W.S. plan for development of a wildlife corridor in south Texas. Important parcels have been identified and a considerable acreage of land upon which dunes sit has been purchased. Restoration can augment the effectiveness of conservation in a number of ways, including the creation of buffers, the increase in the effective size of a conserved parcel, the creation of corridors, and the initiation of a successional trajectory that will eventually result in an ecosystem that is not much different from one at a conserved site.

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